Nosy neighbours: large broods attract more visitors. A field experiment in the pied flycatcher, Ficedula hypoleuca

Article (Accepted Version)

Nosy neighbours: large broods attract more visitors – a field experiment in the pied flycatcher, *Ficedula hypoleuca*

Running headline: SCHUETT ET AL.: PROSPECTING AND BROOD SIZE

Wiebke Schuett[a*], Pauliina E. Järvistö[b], Sara Calhim[b,c], William Velmala[b], Toni Laaksonen[b1]

[a] Zoological Institute, Biocenter Grindel, University of Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany

[b] Section of Ecology, Department of Biology, University of Turku, Turku 20014, Finland

[c] Department of Biological and Environmental Science, University of Jyväskylä, FI-40014, Finland

[*] corresponding author: wiebkesch@googlemail.com; phone: 0049-40-42838-3673

[1]All authors designed the experiment and conducted fieldwork. WS processed the data. WS, SC performed statistics. WS wrote the manuscript; other authors provided editorial advice.

Summary

Life is uncertain. To reduce uncertainty and make adaptive decisions, individuals need to collect information. Individuals often visit the breeding sites of their conspecifics (i.e. “prospect”), likely to assess conspecifics’ reproductive success and to use such information to identify high quality spots for future breeding. We investigated whether visitation rate by prospectors and success of visited sites are causally linked. We manipulated the reproductive success (enlarged, reduced, control broods) in a nest-box population of migratory pied flycatchers, *Ficedula hypoleuca,* in Finland. We measured the visitation rates of prospectors at 87 nest-boxes continuously from manipulation (day 3 after hatching) to fledging. 302 adult pied flycatchers prospected 9194 times on these manipulated nests (at least 78% of detected prospectors were successful breeders). While the number of visitors and visits were not influenced by the relative change in brood size we induced, the resulting absolute brood size predicted the prospecting behaviour: the larger the brood size after manipulation, the more visitors and visits a nest had. The parental provisioning rate at a nest and brood size pre-manipulation did not predict the number of visitors or visits post-manipulation. More visitors, however, inspected early than late nests and broods in good condition. Our study suggests that individuals collect social information when visiting conspecific nests during breeding and provides evidence that large broods attract more visitors than small broods. We discuss the results in light of individual decision-making by animals in their natural environments.

Key-words: brood size; information use; prospecting; RFID; social information

Introduction

In life there are often many options among which to decide. Different options may have very different fitness consequences, so that organisms should favour some over others, depending on the fitness benefits of each option in the current situation. In order to be able to make decisions that maximize fitness, organisms often require information about environmental conditions (e.g. Dall et al. 2005). Information can be obtained by trial-and-error, i.e. from directly interacting with the environment (personal information, e.g. Dall et al. 2005; Danchin et al. 2004), or from observing other organisms interacting with the environment and/or the consequences of their decisions (social information, e.g. Danchin et al. 2004; Seppänen et al. 2007). Individuals should invest into collecting information especially when the upcoming decision can have vast fitness consequences, such as the decision about whether to emigrate and where to breed (e.g. Fuller 2012; Martin 1998). Lizards use social information to make decisions about emigration (Cote and Clobert 2007); and in many bird species individuals visit nests of con- and heterospecifics (reviewed in Reed et al. 1999), possibly in order to assess the success of these nests (heterospecifics: Forsman and Thomson 2008; conspecifics: e.g. Reed et al. 1999). Such information may then be used as an indicator of habitat quality on which to base future breeding decisions. In support of this, migratory pied flycatchers, *Ficedula hypoleuca*, for example, use social information from observing breeding (site) decisions of resident tit species when deciding where to breed (Seppänen et al. 2011) and how much to invest into breeding (Forsman et al. 2012).

Visiting the nests of other individuals is not restricted to the settlement process and the onset of breeding, but is taking place throughout the breeding season (Boulinier et al. 1996; Doligez et al. 2004; Eadie and Gauthier 1985; Ottosson et al. 2001; Ward 2005). It is thought that individuals collect information during the breeding season to guide their breeding habitat decision in the subsequent year (e.g. Danchin et al. 1998; Doligez et al. 2004; Eadie and Gauthier 1985). Theoretical work suggests that a very successful strategy is to assess the reproductive success of conspecifics and to use this information to choose a breeding habitat the next year as long as patch quality is reasonably correlated over time (Doligez et al. 2003). Previous studies that tested these ideas empirically at large scales (e.g.

colony level or large breeding patches) indeed found support for the essential prerequisite, i.e. that local breeding success is autocorrelated among years in colonies (Aparicio et al. 2007; Brown et al. 2000; Danchin et al. 1998) and in breeding patches (Doligez et al. 1999). Furthermore, prospecting increased with colony productivity (Cadiou 1999; Calabuig et al. 2010). Overall, productivity in a colony or patch correlated positively in the next year with patch-specific return rates (Bollinger and Gavin 1989), recruitment of breeders (Danchin et al. 1998), colony growth (Brown et al. 2000) and early settlement rates (Calabuig et al. 2008). Relationships between local productivity and local return rates (or other measures of settlement decisions, including emigration rates) the next year have also been shown experimentally (Aparicio et al. 2007; Boulinier et al. 2008; Doligez et al. 2002; Parejo et al. 2007), suggesting that individuals use social information *per se* when deciding where to breed at a patch or colony scale.

In contrast to the considerable body of literature on breeding site decisions at large scales, few studies have focused on information use for site selection and prospecting at small scales (e.g. territory or small patches, Kivelä et al. 2014). Yet, (breeding) habitat choice is likely a sequential, stepwise process, in which different criteria are hierarchically ordered along different scales (Klopfer and Ganzhorn 1985). Within larger breeding patches there is often variation among nesting sites in reproductive success and such variation is often consistent across years, i.e. some nesting sites are repeatedly more successful than others (e.g. Hoover 2003). Therefore, depending on the spatial scale at which temporal autocorrelation in reproductive success is observed, individuals should not only pay attention to the reproductive success at a large but also at a small scale before deciding where to breed. In line with this prediction, prospecting common goldeneyes, *Bucephala clangula*, were more frequently trapped in successful than unsuccessful nests (Zicus and Hennes 1989). Also, conspecific brood parasitism in common goldeneyes occurred more frequently in those nest sites that had been prospected more frequently in the previous year (Pöysä 2006). Furthermore, prospecting has been shown to increase with parental activity at a nest, with parental activity being predictive of the nest success (Doligez et al. 2004).

Yet, prospectors may directly cue on environmental factors of nest site quality that affect reproductive success, such as food availability or predator presence. For instance, individuals could visit nests of other individuals, not to collect social information about the reproductive success of those individuals, but rather to independently assess some other characteristics of the nest to evaluate the quality of the nest site ("independent assessment theory", Valone and Templeton 2002), i.e. to collect personal information. Similarly, individuals may first use habitat cues to identify high quality spots within an area and maybe only subsequently validate and update the value of this information by also prospecting on the success in the nest. Also, individuals could visit neighbours' nests to increase their familiarity with the neighbourhood (Piper 2011); site familiarity has previously been shown to improve future territory acquisition in juvenile lizards (Stamps 1987) and floating adult birds (Bruinzeel and Van de Pol 2004). However, at least for some environmental aspects, it seems individuals are not able to assess the quality of the breeding site *per se*. For instance, common goldeneye females were not able to assess nest predation risk of new, previously unoccupied nest sites (Pöysä et al. 2001). Instead, they seem to use social information (or own experience) to distinguish between breeding habitats of different quality (Dow and Fredga 1985; Pöysä 1999; Pöysä 2006). Using social information may thus be useful to assess breeding site quality.

To assess whether prospecting and measures of reproductive success are causally linked, experiments are needed. To date, experiments aiming to distinguish between above mentioned possibilities (i.e. collection of social versus personal information during prospecting) are rare: we are only aware of two studies that tested for a causal link between the visits at a nest by conspecifics and nest reproductive success (Parejo et al. 2008; Pärt and Doligez 2003) and those studies were rather limited in sample size and observation duration (3h per nest) for detecting prospecting behaviour.

To tackle the question whether individuals visit conspecifics' nests on the basis of the reproductive success of their neighbours, we experimentally manipulated brood size during the early nestling stage in a wild population of migratory pied flycatchers, *Ficedula hypoleuca*, in Finland and subsequently measured prospecting at the nests throughout the nestling period. Single-brooded pied flycatchers are

ideal model organisms for the study since they frequently visit the nests of their conspecifics during breeding and the identity of prospectors can be known by using RFID (Radio-frequency Identification) tags (Ottosson et al. 2001). Also, the time window for breeding is short for pied flycatchers in Finland due to a migratory schedule. Thus, individuals should quickly decide where to breed when arriving on the breeding grounds. Information collected the previous year could be especially useful here (e.g. Doligez et al. 2004; Pärt et al. 2011). We manipulated brood size after hatching (when chicks were 3 days old), which should be before the prospecting peak as reported in several species (e.g. Boulinier et al. 1996), and measured prospecting behaviour of neighbouring conspecifics continuously until fledging using automated reader systems that recorded the individual RFID tag codes of the prospecting birds. This manipulation enabled us to disentangle the effect of brood size *per se* on prospecting from any other correlated variable (e.g. habitat features) that might be directly linked to prospecting. We predicted that if brood size *per se* determines prospecting behaviour at a nest, nests with enlarged broods should be visited more frequently and by more visitors than those with reduced broods; whereas there should be no or a weaker correlation between the original brood size of the nest and prospecting behaviour post-manipulation. Finally, we examined whether offspring provisioning rate by the parents is correlated with prospecting at a nest, as observed in other species (Doligez et al. 2004; Parejo et al. 2008).

Material and methods

Study population and general monitoring

The experiment was conducted in a nest-box population of pied flycatchers on the Island of Ruissalo, Turku, in Southwest Finland (ca. 60°25'60N, 22°10'0E) in 2012. The study population has been monitored since 2004 and consists of nest-boxes that are situated in forest patches (mainly oak, *Quercus robur*, and Scots pine, *Pinus sylvestris*). In 2012 there were 216 successful pied flycatcher nests

in 436 nest-boxes, spread over an area of ca. 4 km x 1.5 km. Distances between nest-boxes were roughly 30 m.

The study site was visited every morning from the end of April to map the arrival of males (they start singing immediately upon arrival) at the breeding grounds (see Velmala et al. 2015 for details). Males were captured as soon as possible after arrival and settlement (using mist nets and swing-door traps in nest-boxes); females were captured together with the males or at mid-incubation. About 45% of adults were first trapped during breeding, i.e. from egg-laying onwards. Birds were individually marked with aluminium rings (from the Ringing Centre of the Finnish Museum of Natural History) and obtained a small RFID tag (Trovan 100A, Melton, UK), a uniquely coded microchip that was inserted under the skin in the upper back (see Ratnayake et al. 2014). During trapping in 2012, 490 adults obtained or already carried a RFID tag; some additional birds that were not trapped in 2012, but that had obtained RFID tags already in 2010 as adults or chicks, could be later identified from receiver readings (each year about 10-30% of females and 20-40% of males had previously been captured and marked in the study area: Laaksonen, T., unpublished data). RFID tags were read in the field from automated transponder reader systems installed at 87 nest-boxes allowing us to track nest visits by prospectors and parents (see *Prospecting behaviour* and *Parental care: offspring provisioning*).

All nest-boxes were monitored at least twice a week from beginning of May until early July, to determine egg-laying date (flycatchers lay one egg per day), clutch and brood size for each nest (see also *Offspring data*). From the 12th day of incubation the nests were visited daily for determining the hatching date.

Brood size manipulation

When nestlings were 3 days old (hatching day set to day 0), we conducted a brood size manipulation accompanied with a partial brood cross-fostering in 165 of the 216 successful flycatcher nests (see also Järvistö et al. 2015; Järvistö et al. 2016). Based on the final clutch size (number of eggs prior to

hatching) we enlarged (brood size was increased by one; *N* = 52), reduced (brood size was decreased by one; *N* = 56) or maintained the brood size (*N* = 57; "control" = 25, "control-swap" = 32, for details see below). Simultaneously with the brood size manipulation about half of the chicks in a brood were swapped with half of the nestlings in another brood of the same age for the broods in the "reduced", "enlarged" or the "control-swap" group (for more details on swap types see Järvistö et al. 2015). In the second control group, half of the nestlings of a brood were removed from their nests for about 20 min and then returned. For the questions presented here the differentiation between the two control treatments is not relevant, thus we will refer to them together as "control". If, on manipulation day, the brood size of a nest was smaller than its final clutch size (due to unhatched eggs or dead hatchlings), the number of nestlings needed to restore the final clutch size was added to the focal nest using nestlings from non-experimental spare nests of the same age. Subsequently, we conducted the brood size manipulation. To account for any potential effects the time of the season could have on any measures, we conducted manipulations in groups of two nests in which one was enlarged and one reduced on the same day (with only three exceptions; see Online Resource 1, Table S1). Furthermore, we tried to match the number of groups with the number of controls on the same day (see Online Resource 1, Table S1). The assignment to the treatment groups was done randomly such that no spatial aggregations of enlarged or reduced broods were created that could influence prospecting patterns at a large scale. There was no difference in the number of eggs prior to manipulation among the prospective treatment groups (Online Resource 2, Table S2). In accordance with our manipulation, treatment groups differed in their number of offspring post-manipulation and this difference persisted until fledging (Online Resource 2, Table S2).

Offspring data post-manipulation

After the brood size manipulation, we visited nests when hatchlings were 5 and 12 days old to monitor brood sizes. At the age of 12 days we also measured offspring body size (wing length to an accuracy of

0.5 mm) and mass (to an accuracy of 0.1 g). For analyses we used the residuals of the regression between the mean brood mass and the mean brood wing size when the offspring were 12 days old (using data from nests with receivers, see *Prospecting behaviour*) as an estimate of brood condition (see *Statistical analyses*). Finally, when hatchlings were 16 days old, we visited nests daily until fledging to infer the number of fledglings.

Prospecting behaviour

We used automated transponder reader systems (LID-665 decoders, Trovan, Melton, UK) at the nest-boxes which allowed continuous monitoring of all visits by flycatchers with microchips to the nests. The antenna of each receiver was set to surround the nest hole under a plastic cover, which is in position all year round. The birds thus do not notice the appearance of the antenna around the nest hole. Subsequently, the RFID codes of any micro-chipped flycatcher that entered or hung at a nest-box entrance was read and saved by the system. To avoid multiple readings of the same visit, we only used readings of the same RFID code if the time interval between consecutive readings of the same code was 30s or more.

A total of 87 experimental nest-boxes (*N* = 26 enlarged; *N* = 34 reduced; *N* = 27 control) that were spread over a large part of the study area obtained a receiver reading system. RFID readings were recorded from the day of hatching (day 0) until fledging (occurs normally at day 16/17) or until the end of day 17 (which ever was first). There was no difference among the prospective treatment groups in the number of visits or number of visitors per day prior to manipulations (GLMs with negative binomial error structure, controlling for hatching date and number of neighbours and the recording period as offset variable: visitors: χ^2 LR = 2.48, DF = 1, *P* = 0.290; visits: χ^2 LR = 1.89, DF = 2, *P* = 0.388; *N* = 84 nests), indicating that any differences in prospecting among treatment groups post-manipulation was driven by the manipulation *per se.* Furthermore, there was no correlation between either the number of visits or visitors per day prior to manipulation and the number of nestlings prior to manipulation

(GLMs with negative binomial error structure, controlling for hatching date and number of neighbours and the recording period as offset variable: visitors: χ^2 LR = 0.44, DF = 1, P = 0.506; visits: χ^2 LR = 0.14, DF = 1, P = 0.712; N = 84 nests). The absence of such correlation might be because prospecting should be high when the quality of information about reproductive success is also high, i.e. during later breeding stages (Boulinier et al. 1996). Accordingly, the number of visits and visitors was rather low prior to manipulation and increased with chick age (peak around day 9-11, see Online Resource 3, Fig. S1). For the purpose of this study we do not further consider pre-manipulation prospecting data, i.e. we only focus on prospecting data post-manipulation (from the time of manipulation at day 3 onwards). For some reader systems part of the data was missing (battery failure, full memory, technical failure), so that we corrected for the duration of time each reader was recording in analyses (for details see *Statistical analyses*): In 6 cases we had less than 10 days of data post-manipulation (of these: minimum = 6.96 days, maximum = 9.19 days).

We could distinguish visitors from parents at a nest from the number of readings and from multiple trappings at a nest (e.g. during territory establishment; mid-incubation; parents were also trapped when nestlings were 10 days old). We also verified parentage from blood samples collected from adults and nestlings (see Järvistö et al. 2015). Similarly, we were able to determine the breeding nest-box of most visitors (and therefore the distance from the visitors' own nest to the visited nest), even in cases when a nest of a visitor had no receiver reading system (see *Results*).

Parental care: offspring provisioning

When offspring were 9 days old, we measured the number of visits of each parent to their own nest-box for 24h (using data of the receiver reading systems). In order to clearly differentiate this measurement from visits to nests by prospectors, we will refer to visits by parents to their own nests as "offspring provisioning" (as opposed to "visitors" and "visits" respectively which corresponds to prospectors). We decided to measure offspring provisioning rate only on day 9, because we did not

visit, i.e. did not disturb, the nests on this day. 85 (of the 87) receivers were working on day 9: 83 recorded the full 24h (1440 min), the two remaining receivers recorded for 917 and 1050 min respectively. Since the recording period was less than 24h for two nest-boxes, we divided the total number of visits by parents to their own nest by the time the receiver was up (in min) and multiplied this value by 1440 min to obtain the offspring provisioning rate per 24h for each nest (results were qualitatively the same when we discarded the parental data of the two incomplete cases). We obtained data on offspring provisioning from parents in 85 nest-boxes (84 females, 69 males; note that the difference in male and female numbers might be due to secondary nests and/or because females were easier to trap during incubation).

Statistical analyses

We analysed with GLMs whether the brood size manipulation and other variables, such as brood condition, brood size and offspring provisioning post-manipulation, predicted either the number of visitors or the number of visits at a nest-box post-manipulation. We analysed both the number of visitors and number of visits, since, for instance, the number of visitors at a nest may be unaffected by the brood size, but visitors could visit nests with larger brood size more often. Unless stated differently, all models had negative binomial error structures. Models with negative binomial errors controlled for overdispersion and their AICs (Akaike Information Criterion, with lower AIC indicating better model fits, Zuur et al. 2009) were consistently lower compared to models with poisson error structure. Since receivers had recorded for different time periods (see *Prospecting behaviour*), we used the recording period (in minutes, divided by 1440 min to obtain the "receiver recording days") as offset variable (natural logarithm taken) (Zuur et al. 2009). Therefore, model outputs provided estimates for the mean number of visits and visitors respectively per day per nest-box.

We assumed that the number of pied flycatcher neighbours affects the number of visitors and visits at a nest, because a nest with more neighbours has more potential prospectors. Therefore, we calculated

for each nest the number of active pied flycatcher nests (over the whole breeding season) within the median prospecting distance of the population post-manipulation (122m, see *Results*; hereafter: "number of neighbours"). Active nests were those nests that hatched chicks (N = 216). In only four cases did active nests not fledge offspring, thus the number of active nests was also tightly linked to the number of successful nests in the vicinity. We assumed that the number of active pied flycatcher nests was a good proxy for the number of adults carrying RFID chips within the area (note that the number of adults with RFID chips as such was not straightforward to calculate because the number of individuals carrying a chip in the study area changed every day).

All full models contained the number of neighbour nests (see above) and the hatching date as explanatory terms. Both variables were mean centred. The effects of brood size manipulation and number of chicks (at day 12) on nest visitation were assessed in different models due to the obvious association between the variables caused by the experiment (Spearman correlation: R_s = 0.69, P < 0.001, N = 87; see also Online Resource 2, Table S2). The models testing the effect of the number of chicks at day 12 on prospecting also included the brood condition at day 12. The number of offspring and brood condition at day 12 did not correlate (GLM with normal errors; $F_{1,85}$ = 0.38, R = -0.066, P = 0.541, N = 87 nests). We analysed the correlation between the number of hatchlings prior to the manipulation and prospecting in further separate models. Similarly, the relationship between offspring provisioning and prospecting was assessed separately from above models due to a smaller sample size. Note that if all explanatory variables for which the full sample size was available (i.e. brood size manipulation, number of chicks at day 12, brood condition at day 12, number of hatchlings prior to manipulation, hatching date and number of neighbour nests) were included as main effects (no interactions) in one GLM per response variable (i.e. number of visitors and number of visits respectively) we obtained qualitatively the same results compared to separate models reported here.

To obtain minimal adequate models (sensu Crawley 2007), full models were step-wise simplified by taking each term out in turn. At each of these steps we removed the least significant term (as indicated by likelihood ratio tests, see below). A removal of a term was only carried out if it did not significantly

reduce the explanatory power of the model; we tested whether the explanatory power of the model was reduced from each more complex to simpler model with likelihood ratio tests (Crawley 2007). All statistical analyses were conducted in R (R Core Team 2012).

Results

Number of visits and visitors post-manipulation

302 different individuals that carried RFID codes were detected prospecting at the 87 nests with receivers post-manipulation (*N* = 169 males, 127 females, and 6 individuals of unknown sex that had been chipped as chicks in previous years). They prospected altogether 9194 times. Of these prospectors, we could clearly identify the breeding nest-box for 124 males and 118 females. The breeding status of the other individuals was not known (they may have been breeders in e.g. natural cavities or outside the study site, failed breeders or non-breeders). Of the 242 known breeders most were known to be successful (120 males, 115 females; two confirmed failed breeders of each sex). The visitors with known breeding boxes came from a mean distance of 169 m ± 1.9 SE (median: 122 m, range: 16-2665 m, *N* = 6482 prospecting events) when they prospected on the experimental boxes with reader systems. The maximum possible prospecting distance (i.e. maximal distance from a nest-box to a nest-box with receiver) was 4024 m.

Number of visitors per nest-box post-manipulation

The mean number of visitors per nest-box per day post-manipulation did not significantly differ among the brood size manipulation groups (Table 1, model 1a, Fig. 1a) even though differences between them followed the predicted direction (see Fig. 1a): reduced broods were estimated to have on average 9% less visitors than enlarged broods (see model 1a; for enlarged broods: exp(0.602)*13 days mean recording time = 24 visitors, for reduced broods: exp(0.493)*13 days mean recording time = 21

visitors). Nevertheless, the manipulation was effective in that the number of chicks post-manipulation predicted prospecting behaviour: the number of visitors increased with the number of offspring (on day 12; Table 1, model 1b, Fig. 2a). The number of hatchlings prior to the manipulation, on the other hand, did not predict the number of visitors at a nest post-manipulation (GLM with negative binomial error structure, hatch date and number of neighbours as covariates: χ^2 *LR* = 0.01, DF = 1, *P* = 0.917, *N* = 87). These results together suggest that the observed relationship between brood size and number of visitors was driven by our brood size manipulation. The absence of a significant effect of the manipulation *per se* (despite an effect of the resulting number of nestlings) might be explained by low power (for details see Online Resource 4): the likelihood of detecting an effect of the brood size manipulation (a difference of one chick between the treatments) on the mean number of daily visitors was 22.6 %; the likelihood of detecting an effect of the absolute number of offspring (resulting from the brood size manipulation) was twice as high (46.6 %).

The number of visitors at a nest also increased with mean brood condition (on day 12; Table 1, model 1b; Fig. 2b), and with the number of neighbours (Table 1, model 1a & 1b). Earlier nests were visited by more individuals than later nests (Table 1, models 1a & 1b; Fig. 3a). The offspring provisioning rate (when offspring were 9 days old) did not predict the number of visitors at a nest-box (GLM with negative binomial error structure, hatch date and number of neighbours as covariates: χ^2 *LR* = 0.37, DF = 1, *P* = 0.543, *N* = 85).

Number of visits per nest-box post-manipulation

The mean daily number of visits by prospectors at a nest did not depend on the brood size manipulation group (Table 2, model 2a, Fig. 1b) even though the variation between manipulation groups did again point towards the predicted directions (see Fig. 1b). Reduced broods were estimated to have on average 94 visits, enlarged broods 114 visits over the mean receiver recording period (see model 2a; for enlarged broods: exp(2.167)*13 days mean recording time; for reduced broods:

exp(1.978)*13 days). The number of visits by prospectors increased with increasing number of nestlings in a nest at the age of 12 days (Table 2, model 2b, Fig. 2c). Again, the number of hatchlings prior to the brood size manipulation was unrelated to the number of visits at the nest post-manipulation (GLM with negative binomial error structure, hatch date and number of neighbours as covariates: χ^2 *LR* = 0.32, DF = 1, *P* = 0.572, *N* = 87 nests), indicating that the relationship between the number of offspring post-manipulation and the number of prospecting visits was a result of the manipulation. The power for detecting an effect of the manipulation *per se* was again half the power of detecting an effect of the number of offspring post-manipulation (manipulation: 26.4 %; number of offspring at day 12: 51.8 %; for details see Online Resource 4). This might again explain why no significant effect of the manipulation, only of the resulting number of offspring was observed.

In contrast to the number of offspring at day 12, brood condition at day 12 was not linked to the number of visits at a nest post-manipulation (Table 2, model 2b; Fig. 2d). Yet, earlier broods were visited more frequently by prospectors than later broods (Table 2, model 2a & 2b; Fig. 3b); the number of visits also increased with the number of neighbours (Table 2, model 2a & 2b). The offspring provisioning rate at a nest did not correlate with the number of visits at this nest-box (GLM with negative binomial error structure, hatch date and number of neighbours as covariates: χ^2 *LR* = 0.19, DF = 1, *P* = 0.665, *N* = 85).

Discussion

We conducted a brood size manipulation experiment to tease apart whether pied flycatchers visit conspecific nests to cue on their reproductive output *per se* (i.e. collect social information) and not some aspect of the environment (e.g. habitat quality) correlated with it (i.e. collect personal information). The relative change in brood size by one chick, i.e. the manipulation *per se* (reduced or increased), did not significantly influence visitation at a nest-box, yet the absolute number of nestlings resulting from the manipulation predicted both the number of visits and number of visitors. A low

power likely caused the manipulation effect *per se* to be non-significant. This interpretation is also supported by the fact that variation in prospecting among manipulation groups pointed towards the predicted directions (enlarged groups with more visitors and visits than reduced groups; Fig. 1). That the number of nestlings pre-manipulation did not predict visitation patterns post-manipulation while the number post-manipulation did, suggests that the original differences in nestling number between nest sites due to e.g. territory quality had less effect on prospecting than the final number of nestlings post-manipulation. Visitation of nests with young nestlings was rather low and there was no correlation between visitation and brood size prior to manipulation. Together, these results indicate that pied flycatchers are more interested in conspecific nests with larger brood size than in those with smaller brood size, especially when chicks in the nests are old (i.e. the quality of information on the reproductive success is high, see Boulinier et al. 1996). This suggests that pied flycatchers may collect social information on the reproductive success of conspecifics or information through the reproductive success of conspecifics when visiting their nests. Furthermore, brood condition predicted the number of visitors (but not number of visits) at a nest, while offspring provisioning did not correlate to either measure of visitation, potentially indicating that the pied flycatchers did not use the offspring provisioning rate of parents as an indicator of brood size. Broods that hatched earlier in the season were visited more often and by more visitors than later broods, suggesting earlier broods are more attractive to prospectors. Finally, a large number of successful breeders visited conspecific nests. Many previous studies, in which prospecting was monitored by observing nests from a distance rather than by automatic tracking, identified mainly unsuccessful or non-breeders as visitors (e.g. Doligez et al. 2004; Parejo et al. 2008; Reed et al. 1999). These seemingly contradictory results between studies might arise from different biological characteristics of the study species, different methods used and/or variation in environmental conditions. For instance, environmental conditions in 2012 were favourable for pied flycatchers (cf. low breeding failure we reported here) which may have resulted in few failed breeders that could prospect compared to previous studies on collared flycatchers. Furthermore, it is important to note that we did not examine how often unsuccessful or non-breeders

prospected; our data only show that breeders frequently do this. Our study suggests that visiting conspecific nests is a source of information for successful breeders to potentially identify better sites than their current one for future breeding.

In our study, the number of visitors and number of visits at a nest were positively correlated with the number of nestlings post-manipulation, indicating that highly successful breeding sites are identified via the reproductive success of nests. An alternative explanation for our results could be that prospectors spent less time at nest-boxes with smaller broods than larger broods and that those short visits were less likely to be recorded by our system. This explanation is, however, unlikely because we verified from videos that even very short visits (1-3s; by parents) are reliably recorded by our system (Schuett et al. unpublished data). Our prospecting results are in line with previous studies that experimentally showed that individuals cue on the reproductive success of conspecifics. However, while previous studies have investigated this link mainly at large (patch) scales (Aparicio et al. 2007; Boulinier et al. 2008; Doligez et al. 2002; Parejo et al. 2007), we provide evidence that conspecific reproductive success is also important at small, i.e. territorial, scale. Our results corroborate findings of the only two experimental studies conducted at the territory scale (Parejo et al. 2008; Pärt and Doligez 2003). When the brood size was reduced in spotless starlings, *Sturnus unicolor*, fewer visits at nests with old nestlings were observed compared to control broods (Parejo et al. 2008) and an increase in brood size in collared flycatchers increased the probability that a visitor was seen at a nest in comparison to control broods (Pärt and Doligez 2003). Taken together, these studies at different scales suggest that decision-making is a hierarchical process (sensu Klopfer and Ganzhorn 1985): individuals may first use social information at a large scale, to identify high quality areas for (future) breeding, and subsequently collect information at a small scale, in order to detect those breeding sites within high quality patches that are highly successful.

Not only the quantity but also the quality of nestlings predicted the number of visitors. The condition (relative mass) of fledglings is an important factor influencing the survival of flycatchers (Lindén et al. 1992; Lundberg and Alatalo 1992). Therefore, the quality of nestlings could also be used as proxy for

the quality of a nest site by visitors. In accordance with this, Doligez et al. (2002) also highlighted a role of offspring quality on social information use: while the immigration rate at patch level increased only with nestling quantity, the emigration rate at patch level increased both with low quantity and low quality of nestlings. Experiments manipulating chick condition at the territory scale would be now required to assess whether chick condition *per se* influences prospecting at a nest site scale.

We found no correlation between nestling number and condition while we detected positive correlations between the number of visitors and both the quality and quantity of nestlings. This contrasts with the general trade-off between offspring number and condition (e.g. Nager et al. 2000). Our results might be due to favourable environmental conditions in the year of the experiment, such that brood condition was not affected by our brood size manipulation. This interpretation is in line with the low brood failure we observed during the breeding season.

Alternatively to the brood size (or brood quality) *per se*, offspring provisioning rates by parents could influence the visitation patterns by prospectors at a nest (Doligez et al. 2004). Yet, we did not find correlations between offspring provisioning rates and visitation. Similarly, the probability that collared and pied flycatchers visited tit nests did not depend on the offspring provisioning rate by the parents of the prospected nest (Forsman and Thomson 2008). These results contrast with findings from two other collared flycatcher studies (Doligez et al. 2004; Pärt and Doligez 2003), where the probability of observing a visitor at a nest was higher in nests with high parental care (offspring provisioning and vigilance). In lesser kestrels, *Falco naumanni*, visitation was associated, but not linearly, with offspring provisioning: it increased but then decreased with increasing offspring provisioning (Calabuig et al. 2010). Finally, in spotless starlings, offspring provisioning correlated to visitation frequency, but brood size was a better predictor of visitation frequency than offspring provisioning (Parejo et al. 2008). Taken together, these results suggest that offspring provisioning by parents might attract prospectors to a certain extent (it indicates the presence of a successful nest). Yet, parental provisioning rate might only provide a rough estimate of the reproductive success of a nest since parental provisioning rate is variable over time and may also depend on the amount of food carried in a given visit (see also

discussion in Parejo et al. 2008). In contrast, brood size provides more reliable information on the reproductive success that year. If this was not the case, individuals could just observe parental provisioning from a distance (Parejo et al. 2008). This again could suggest that decision-making is a hierarchical process. Once highly successful large patches are identified, successful nests within those patches are located by looking for parents attending their own nests, and finally information on the actual reproductive success of these nests is collected by visiting the nests. Revisits at later nest stages might then be used to update the previously collected information, unless individuals are able to assess the rough age and/or number of nestlings externally (e.g. via characteristics of the begging calls). In the latter case, prospecting at previously identified active nests (e.g. via parental activities) may occur mainly when hatchlings are older and brood sizes are large (i.e. no need for many revisits at a nest) to obtain reliable information on reproductive success. Alternatively, or additionally, it should be noted that we mainly followed the prospecting behaviour of successful breeders, while some of the previous studies followed mainly non- or failed breeders (e.g. Doligez et al. 2004). These two groups of individuals might differ in their information sampling and information use (for general discussion see e.g. Ponchon et al. 2013), potentially explaining seemingly contradicting results discussed above. In future work we will need to identify prospecting patterns on an individual level to shed light on underlying mechanisms and how those might differ for individuals of different sex, breeding status (e.g. non-breeder, failed breeder, more or less successful breeder) or experience (first year or older breeder) in our system. This will allow a more in-depth comparison with results in other species and an estimation of the generality of patterns found.

Earlier broods were more attractive to visitors than later broods. Earlier broods are generally more successful than later broods in birds (e.g. Brooke 1979; Elmberg et al. 2005), including pied flycatchers (Lundberg and Alatalo 1992). Furthermore, male pied flycatchers that arrive early at the breeding grounds monopolise high quality breeding sites are preferred by females (Alatalo et al. 1986), breed earlier, and have direct fitness benefits over late arriving males (Velmala et al. 2015). Therefore, if early broods are on average more successful and are produced in high quality breeding sites, individuals

should especially invest into collecting social information from early nests and use this information the following year when choosing a nest site. Similar to our findings, Doligez et al. (2004) observed that the probability that a nest was visited decreased over the breeding season.

More studies are now needed to identify whether and how individuals use the collected intraspecific social information in the next year (or even during the current season, for instance to adjust their own parental provisioning behaviour). At a large scale there is quite good evidence that previously successful colonies or patches are preferentially used by breeders the next year (Schjørring et al. 1999, see also *Introduction*). On a small scale, we lack knowledge on the mechanisms that underlie the actual breeding-site choice. Although based on a very small sample size, results by Pärt and Doligez (2003) suggest that visitors breed closer to the nest sites they visited the previous year than to their old breeding site. Along similar lines, Pärt et al. (2011) found most visitors to breed in a site where they had prospected the year before; the reproductive success of these individuals was higher compared to the success of other individuals of the same age. Yet, it is not clear, for instance, how individuals actually choose their breeding site the next year. In migratory species, some preferred territories might be already occupied, so that arriving males might not be able to establish a territory in a previously identified high quality spot. Similarly, females might be restricted in their choice, as they cannot settle in a previously highly successful territory if no male is around yet (Arlt and Pärt 2008).

Here, we experimentally showed that migratory pied flycatchers were especially attracted to highly successful nests, suggesting that they collect information on the reproductive success of their conspecifics when visiting their nests. Studies are now needed to identify how this social information is integrated into future decision-making such as the search for and selection of a breeding site the following year to shed further light on mechanisms of decision-making in the wild. It is still largely unknown, when individuals use the social information gathered from prospecting, especially information that is collected at the small scale.

Acknowledgements

We thank Matias Ukkola, Kirsi Ukkola and Jenna Ruohonen for assistance in the field. The project was funded by the Academy of Finland (grants to TL). We are grateful to Hannu Pöysä, Blandine Doligez and an anonymous reviewer for their constructive comments.

Ethical Approval

All applicable national guidelines for the care and use of animals were followed. The procedures had been approved by the Animal Experiment Board of Finland (animal experiment committee of Southern Finland, ID: VARELY/338/07.01/2012).

Data accessibility: Raw data are provided in the Electronic Supplementary Material (Online Resource 5, Table S4).

Conflict of Interest: The authors declare that they have no conflict of interest.

References

Alatalo RV, Lundberg A, Glynn C (1986) Female pied flycatchers choose territory quality and not male characteristics. Nature 323:152-153

Aparicio J, Bonal R, Muñoz A (2007) Experimental test on public information use in the colonial Lesser Kestrel. Evolutionary Ecology 21:783-800

Arlt D, Pärt T (2008) Sex-biased dispersal: A result of a sex difference in breeding site availability. American Naturalist 171:844-850. doi: 10.1086/587521

Bollinger EK, Gavin TA (1989) The effects of site quality on breeding-site fidelity in bobolinks. The Auk 106:584-594

Boulinier T, Danchin E, Monnat JY, Doutrelant C, Cadiou B (1996) Timing of prospecting and the value of information in a colonial breeding bird. Journal of Avian Biology 27:252-256

Boulinier T, McCoy KD, Yoccoz NG, Gasparini J, Tveraa T (2008) Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. Biology Letters 4:538-540

Brooke MDL (1979) Differences in the quality of territories held by wheatears (*Oenanthe oenanthe*). Journal of Animal Ecology 48:21-32. doi: 10.2307/4097

Brown CR, Brown MB, Danchin E (2000) Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. Journal of Animal Ecology 69:133-142. doi: 10.1046/j.1365-2656.2000.00382.x

Bruinzeel LW, Van de Pol M (2004) Site attachment of floaters predicts success in territory acquisition. Behavioral Ecology 15:290-296

Cadiou B (1999) Attendance of breeders and prospectors reflects the quality of colonies in the Kittiwake *Rissa tridactyla*. Ibis 141:321-326

Calabuig G, Ortego J, Aparicio JM, Cordero PJ (2008) Public information in selection of nesting colony by lesser kestrels: which cues are used and when are they obtained? Animal Behaviour 75:1611-1617

Calabuig G, Ortego J, Aparicio JM, Cordero PJ (2010) Intercolony movements and prospecting behaviour in the colonial lesser kestrel. Animal Behaviour 79:811-817

Cote J, Clobert J (2007) Social information and emigration: lessions from immigrants. Ecology Letters 10:411-417. doi: 10.1111/j.1461-0248.2007.01032.x

Crawley MJ (2007) The R book. John Wiley & Sons Ltd, Chichester

Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends Ecol. Evol. 20:187-193

Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79:2415-2428

Danchin E, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: From nosy neighbors to cultural evolution. Science 305:487-491

Doligez B, Cadet C, Danchin E, Boulinier T (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. Animal Behaviour 66:973-988. doi: 10.1006/anbe.2002.2270

Doligez B, Danchin E, Clobert J (2002) Public information and breeding habitat selection in a wild bird population. Science 297:1168-1170

Doligez B, Danchin E, Clobert J, Gustafsson L (1999) The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. Journal of Animal Ecology 68:1193-1206

Doligez B, Pärt T, Danchin E (2004) Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? Animal Behaviour 67:457-466. doi: 10.1016/j.anbehav.2003.03.010

Dow H, Fredga S (1985) Selection of nest sites by a hole-nesting duck, the Goldeneye *Bucephala clangula*. Ibis 127:16-30. doi: 10.1111/j.1474-919X.1985.tb05034.x

Eadie JM, Gauthier G (1985) Prospecting for nest sites by cavity-nesting ducks of the Genus *Bucephala*. The Condor 87:528-534

Elmberg J, Nummi P, Pöysä H, Gunnarsson G, Sjöberg K (2005) Early breeding teal *Anas crecca* use the best lakes and have the highest reproductive success. Annales Zoologici Fennici 42:37-43

Forsman JT, Seppänen J-T, Nykänen IL (2012) Observed heterospecific clutch size can affect offspring investment decisions. Biology Letters 8:341-343. doi: 10.1098/rsbl.2011.0970

Forsman JT, Thomson RL (2008) Evidence of information collection from heterospecifics in cavity-nesting birds. Ibis 150:409-412

Fuller RJ (2012) Birds and habitat: relationships in changing landscapes. Cambridge University, Cambridge

Hoover JP (2003) Decision rules for site fidelity in a migratory bird, the prothonotary warblers. Ecology 84:416-430. doi: 10.1890/0012-9658(2003)084[0416:DRFSFI]2.0.CO;2

Järvistö PE, Calhim S, Schuett W, Velmala W, Laaksonen T (2015) Foster, but not genetic, father plumage coloration has a temperature-dependent effect on offspring quality. Behavioral Ecology and Sociobiology 69:335-346. doi: 10.1007/s00265-014-1846-0

Järvistö PE, Calhim S, Schuett W, Velmala W, Laaksonen T (2016) Sex-dependent responses to increased parental effort in the pied flycatcher. Behavioral Ecology and Sociobiology 70:157-169. doi: 10.1007/s00265-015-2034-6

Kivelä SM et al. (2014) The past and the present in decision-making: the use of conspecific and heterospecific cues in nest site selection. Ecology 95:3428-3439. doi: 10.1890/13-2103.1

Klopfer PH, Ganzhorn JU (1985) Habitat selection: behavioral aspects. In: Cody ML (ed) Habitat selection in birds, pp 435-453. Academic Press, London

Lindén M, Gustafsson L, Pärt T (1992) Selection on fledging mass in the collared flycatcher and the great tit. Ecology 73:336-343. doi: 10.2307/1938745

Lundberg A, Alatalo RV (1992) The pied flycatcher. Poyser, London

Martin TE (1998) Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656-670. doi: 10.1890/0012-9658(1998)079[0656:AMPOCS]2.0.CO;2

Nager RG, Monaghan P, Houston DC (2000) Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. Ecology 81:1339-1350. doi: 10.1890/0012-9658(2000)081[1339:WCTOBT]2.0.CO;2

Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol. Rev. 82:591-605. doi: 10.1111/j.1469-185X.2007.00027.x

Ottosson U, Backman J, Smith HG (2001) Nest-attenders in the pied flycatcher (*Ficedula hypoleuca*) during nestling rearing: A possible case of prospective resource exploration. The Auk 118:1069-1072

Parejo D, Perez-Contreras T, Navarro C, Soler JJ, Aviles JM (2008) Spotless starlings rely on public information while visiting conspecific nests: an experiment. Animal Behaviour 75:483-488

Parejo D, White J, Clobert J, Dreiss A, Danchin E (2007) Blue tits use fledgling quantity and quality as public information in breeding site choice. Ecology 88:2373-2382

Pärt T, Arlt D, Doligez B, Low M, Qvarnström A (2011) Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. Journal of Animal Ecology 80:1227-1235

Pärt T, Doligez B (2003) Gathering public information for habitat selection: prospecting birds cue on parental activity. Proceedings of the Royal Society B: Biological Sciences 270:1809-1813. doi: 10.1098/rspb.2003.2419

Piper W (2011) Making habitat selection more “familiar”: a review. Behavioral Ecology and Sociobiology 65:1329-1351

Ponchon A et al. (2013) Tracking prospecting movements involved in breeding habitat selection: insights, pitfalls and perspectives. Methods in Ecology and Evolution 4:143-150. doi: 10.1111/j.2041-210x.2012.00259.x

Pöysä H (1999) Conspecific nest parasitism is associated with inequality in nest predation risk in the common goldeneye (*Bucephala clangula*). Behavioral Ecology 10:533-540. doi: 10.1093/beheco/10.5.533

Pöysä H (2006) Public information and conspecific nest parasitism in goldeneyes: targeting safe nests by parasites. Behavioral Ecology 17:459-465

Pöysä H, Ruusila V, Milonoff M, Virtanen J (2001) Ability to assess nest predation risk in secondary hole-nesting birds: an experimental study. Oecologia 126:201-207. doi: 10.1007/s004420000512

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/

Ratnayake CP, Morosinotto C, Ruuskanen S, Villers A, Thomson RL (2014) Passive Integrated Transponders (PIT) on a small migratory passerine bird: absence of deleterious short and long-term effects. Ornis Fennica 91:244-255

Reed JM, Boulinier T, Danchin E, Oring LW (1999) Informed dispersal: prospecting by birds for breeding sites. Current Ornithology 15:189-259

Schjørring S, Gregersen J, Bregnballe T (1999) Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. Animal Behaviour 57:647-654

Seppänen J-T, Forsman JT, Mönkkönen M, Krams I, Salmi T (2011) New behavioural trait adopted or rejected by observing heterospecific tutor fitness. Proceedings of the Royal Society B: Biological Sciences 278:1736-1741. doi: 10.1098/rspb.2010.1610

Seppänen JT, Forsman JT, Mönkkönen M, Thomson RL (2007) Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88:1622-1633

Stamps JA (1987) The effect of familiarity with a neighborhood on territory acquisition. Behavioral Ecology and Sociobiology 21:273-277

Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci. 357:1549-1557

Velmala W et al. (2015) Natural selection for earlier male arrival to breeding grounds through direct and indirect effects in a migratory songbird. Ecology and Evolution 5:1205-1213. doi: 10.1002/ece3.1423

Ward MP (2005) Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information. Oecologia 145:650-657

Zicus M, Hennes SK (1989) Nest prospecting by common goldeneyes. The Condor 91:807-812

Zuur AF, Ieno EN, Walker N, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer

Table 1: Summary of results of GLMs with negative binomial error structures and number of visitors at a nest as response variable. The duration the receiver was recording was added as offset variable (for more details see main text). The effect of brood size manipulation (BSM; model 1a) and number of chicks (model 1b) were assessed in two different models due to a link between the variables (see Online Resource 2, Table S2; main text). Significant *P*-values shown in bold. Estimates (coefficients and their SE) are on the natural log scale. centr., mean centred variable.

Model	N	Explanatory variable	Factor level	Coeff.[a]	SE	χ^2 LR	DF	P
1a	87	(Intercept)	[BSM = control]	0.56 (0.598)	0.04 (0.06)			
		BSM				2.07	2	0.355
			enlarged	(0.004)	(0.09)			
			reduced	(-0.105)	(0.09)			
		Hatching date (centr.)		-0.037 (-0.038)	0.01 (0.01)	6.85	1	**0.009**
		No. neighbours (centr.)		0.045 (0.044)	0.01 (0.01)	18.30	1	**<0.001**
1b	87	(Intercept)		0.055	0.03			
		Brood condition d12 (centr.)		0.170	0.07	6.17	1	**0.013**
		No. chicks d12 (centr.)		0.072	0.03	4.61	1	**0.032**
		Hatching date (centr.)		-0.031	0.01	5.18	1	**0.023**
		No. neighbours (centr.)		0.040	0.01	15.83	1	**<0.001**

[a] coeff, estimates for variables in minimal adequate model, in brackets: coefficients for variables in full model (if no coefficients in brackets: minimal model = full model)

Table 2: Summary of results of GLMs with negative binomial error structures and number of visits at a nest as response variable. The duration the receiver was recording was added as offset variable (for more details see main text). The effect of brood size manipulation (BSM; model 2a) and number of chicks (model 2b) were assessed in two different models due to a link between the variables (see Online Resource 2, Table S2; main text). Significant *P* -values shown in bold. Estimates (coefficients and their SE) are on the natural log scale. Centr., mean centred variable.

Model	N	Explanatory variable	Factor level	Coeff.[a]	SE	χ^2 LR	DF	P
2a	87	(Intercept)	[BSM = control]	2.07 (2.084)	0.05 (0.09)			
		BSM				2.42	2	0.298
			enlarged	(0.083)	(0.13)			
			reduced	(-0.106)	(0.12)			
		Hatching date (centr.)		-0.115 (-0.117)	0.02 (0.02)	30.49	1	**<0.001**
		No. neighbours (centr.)		0.036 (0.036)	0.01 (0.01)	6.30	1	**0.012**
2b	87	(Intercept)		2.063 (2.061)	0.31 (0.05)			
		Brood condition d12 (centr.)		(0.123)	(0.1)	1.70	1	0.192
		No. chicks d12 (centr.)		0.116 (0.119)	0.05 (0.05)	5.97	1	**0.015**
		Hatching date (centr.)		-0.117 (-0.111)	0.02 (0.02)	32.96	1	**<0.001**
		No. neighbours (centr.)		0.036 (0.031)	0.01 (0.01)	6.35	1	**0.012**

[a] coeff, estimates for variables in minimal adequate model, in brackets: coefficients for variables in full model (if no coefficients in brackets: minimal model = full model)

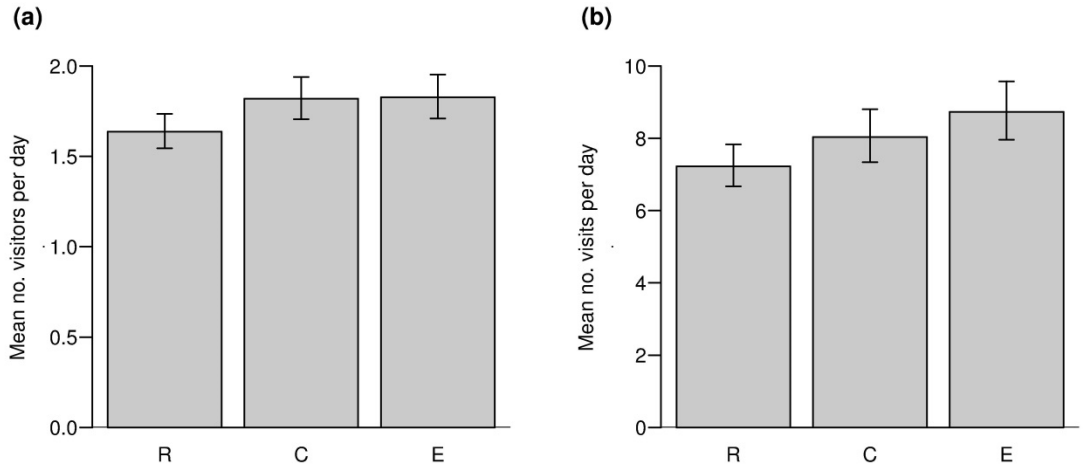

Fig. 1 Mean number (± SE) of (a) visitors and (b) visits per day per nest after brood size manipulation (R, reduced; C, control; E, enlarged) in pied flycatchers. Means (± SE) were calculated from the coefficients from models 1a and 2a (Table 1 and Table 2) and thus represent estimates for nest-boxes of average hatch date and number of neighbours. Standardised effect sizes and their 95% CIs (Nakagawa and Cuthill 2007) were: (a) enlarged: d=0.011 [-0.53, 0.55], reduced: d=-0.27 [-0.77, 0.24], (b) enlarged: d=0.14 [-0.40, 0.68], reduced: d=-0.19 [-0.70, 0.31].

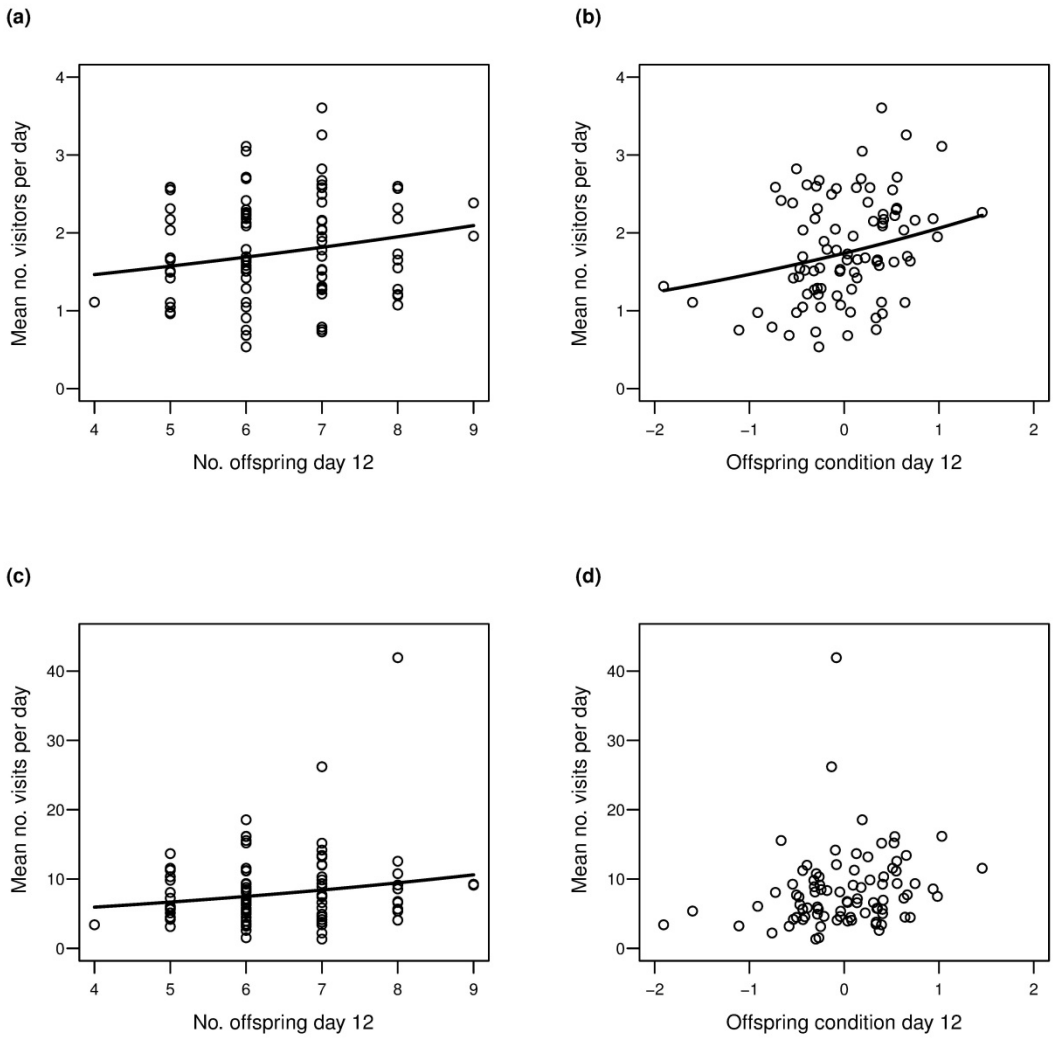

Fig. 2 Mean number of (a, b) visitors and (c, d) visits per day per nest after brood size manipulation in relation to (a, c) the brood size (at day 12) and (b, d) the mean offspring condition per brood (at day 12). As an index of offspring condition the residuals of the regression between the brood mean mass at day 12 and brood mean wing length at day 12 were used. Predicted relationships were obtained from models 1b and 2b (Table 1 and Table 2) and thus represent the relationships for nest-boxes of average hatch date and number of neighbours (as well as mean offspring condition (a) and mean number of offspring (b)). Standardised effect sizes and their 95% CIs (Nakagawa and Cuthill 2007) were: (a) r=0.24 [0.026, 0.45], (b) r=0.27 [0.059, 0.49], (c) r=0.28 [0.064, 0.49], (d) r=0.14 [-0.073, 0.3].

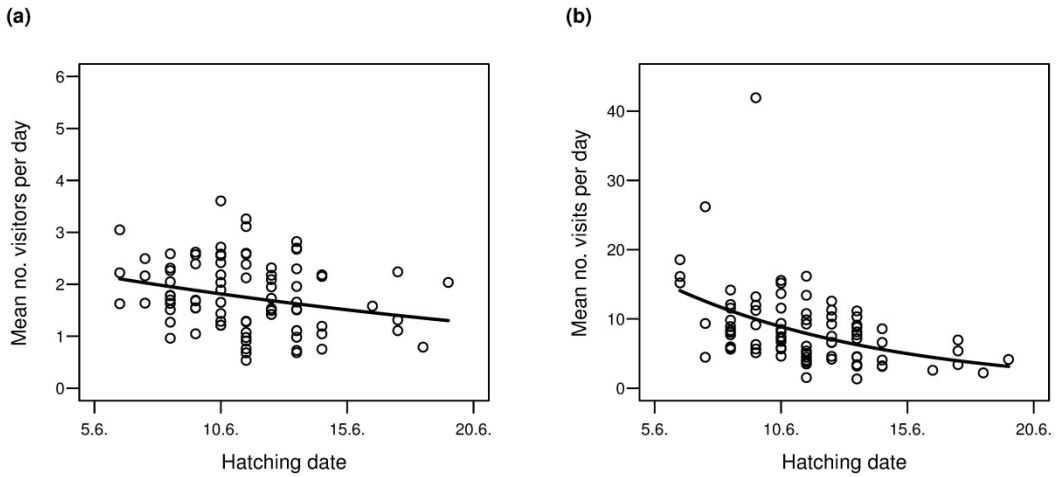

Fig. 3 Mean number of (a) visitors and (b) visits per day post brood size manipulations for nests with different hatching dates (for the mean number of neighbours). Predicted relationships using backtransformed estimates obtained from models 1b and 2b (Table 1 and Table 2) and they thus represent the relationship for nest-boxes with the average number of neighbours.